Limited surrogacy between predatory arthropods along an altitudinal gradient in subtropical rainforest

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ABSTRACT

Biodiversity surveys are often forced to regard single taxa as surrogates for other groups within the same guild. Recently, concerns regarding impacts of climate change have driven a large body of research involving assemblage changes across elevational gradients. Such gradients have commonly been used to investigate changes within invertebrate assemblages, however, surrogacy of patterns displayed between taxa are rarely tested. Without sufficient testing of surrogacy among invertebrate groups, the impacts of described patterns in an ecosystem context, and their implications for biodiversity, remain either unknown or misinterpreted. To address this issue, we investigated changes in the communities of three different groups of predatory epigaeic arthropods, ants, predatory beetles and spiders, along an altitudinal gradient in subtropical rainforest in south-eastern Queensland, Australia. Predatory arthropods were sampled with pitfall traps at four replicate plots at each of five elevations; 300, 500, 700, 900 and 1100 m above sea level (a.s.l.). The three groups displayed differential responses to altitude. Ants responded most clearly with a decline in species richness and progressive change in composition with increasing altitude with depauperate fauna at the highest elevation. Beetles were abundant and species rich throughout the gradient although they were most speciose at 900 m a.s.l. Beetle assemblages progressively changed from low to high elevations, but assemblages at the highest elevation were distinct due to numerous species restricted to this altitude. The abundance and species richness of spiders were similar throughout the gradient, but spiders were distinctly separated into low (300-700 m a.s.l.) and high (900-1100 m a.s.l.) altitude assemblages. Our results indicate that predictions about the impacts of climate change on ecosystem processes such as predation will vary, especially at the highest elevations, according to taxonomic group sampled.

INTRODUCTION

Elevational gradients are characterised by predictable changes in local climatic variables such as temperature, precipitation and humidity (Barry 1992), which make them ideal for investigating the impacts of climate change upon assemblages of species (Richardson *et al.* 2005; Botes *et al.* 2006; Shoo *et al.* 2006). Distributions of organisms are strongly influenced by detectable climatic niches or envelopes (Bakkenes *et al.* 2002; Araujo *et al.* 2004, 2005; Bomhard *et al.* 2005). In montane ecosystems, changes in altitude significantly affect climatic niches and in turn species' distributions and community composition (Walther *et al.* 2002). In habitats such as rainforest, which contain extremely diverse invertebrate fauna, species turnover across elevational gradients can be substantial with unique fauna found at higher elevations (Fisher 1998; Bruhl *et al.* 1999).

Rainforest invertebrates exhibit very high abundance and diversity, occupying a large range of microhabitats and ecological niches (Stork 1993). As a result, they are known to play essential roles in many ecological processes including predation, pollination, herbivory and soil decomposition (Speight *et al.* 1999). Ecological studies often categorise invertebrates into various trophic levels or guilds as a means of relating their relevance to ecosystem functioning (e.g. Hammond 1990; Andrew & Hughes 2004; Gray *et al.* 2007; Grimbacher & Stork 2007). Invertebrates belonging to different trophic levels have already been demonstrated to exhibit varied sensitivities to climatic factors (Voigt *et al.* 2003), however, there has been little subsequent research into the potential impacts of climate change on invertebrate trophic groups. Whilst solid frameworks exist regarding general mechanisms driving certain changes in herbivorous assemblages within rainforest environments, much work is still required regarding predatory invertebrates (Kitching 2006). Insight regarding climate change impacts on predatory rainforest invertebrates can be gathered through assessing changes in predatory assemblages within elevational gradients.

Assemblages of predatory invertebrates have been sampled across elevational gradients in several studies (Olson 1994; Bruhl *et al.* 1999; Botes *et al.* 2006). Many such studies focus on particular invertebrate taxa such as ants (e.g. Fischer 1998), spiders (e.g. Chatzaki *et al.* 2005) or opiliones (Almeida-Neto *et al.* 2006). This single taxon approach is often adopted due to the taxonomic impediment associated with processing large catches of multiple invertebrate groups (Kotze & Samways 1999; Progar & Schowalter 2002). Studies of single taxa inevitably raise the question of surrogacy: to what extent can the patterns observed in one taxon be assumed in others? Clearly groups with limited surrogacy demonstrate trends that cannot be extrapolated to other taxa (Kotze & Samways 1999). Thus, it is imperative to not only understand assemblage patterns across elevational gradients but also the surrogacy of such patterns between similar taxa in similar habitats. In order to confidently identify the level of surrogacy between groups, simultaneous study of multiple taxa must be performed.

In this study a multi-taxa approach was used to assess patterns within predatory guilds across an elevational gradient. Three taxa were examined: Formicidae (ants), predatory Coleoptera (beetles) and Araneae (spiders). In order to determine the level of surrogacy displayed between these predatory groups, patterns of abundance, species richness, and compositional change were examined across an elevational gradient.

METHODS

Study site and sampling methods

This study was conducted as part of the IBISCA-Queensland Project (Kitching *et al.* 2011), which investigated the distributional patterns of a wide range of invertebrate groups along an elevational transect from approximately 300 to

1100 m above sea level (a.s.l.). This transect was established within continuous rainforest in the West Canungra Creek catchment of Lamington National Park, south-east Queensland, Australia (28°09'–28°16'S, 153°06'–153°11'E). The elevational gradient was subdivided into five levels of altitude (viz. 300, 500, 700, 900, 1100 m a.s.l.), each with four replicated plots within an elevational range of 90 m a.s.l. (see Kitching *et al*. 2011 for the precise altitudes of plots). All plots were located within rainforest but the structural type and floristic composition of the rainforest changes with altitude. Plots at 300 m a.s.l. were located within araucarian complex notophyll vine forest, those at 500 and 700 m a.s.l. in warm subtropical complex notophyll vine forest, those at 900 m a.s.l. in cool subtropical complex notophyll vine forest and those at 1100 m a.s.l. in microphyll fern forest with a canopy dominated by Antarctic beech (*Nothofagus moorei*) (Laidlaw *et. al*. 2011a). The IBISCA-Queensland transect also encompasses different climate and soil properties, which are summarised in Strong *et al*. (2011).

Each plot consisted of a 20 x 20 m quadrat. Plots within each altitude were separated by at least 400 m. Plots were established away from significant tree falls or light gaps, at least 50 m from permanent water sources, and did not have a known history of anthropogenic disturbance.

Within each quadrat, we installed nine pitfall traps in a 5 x 5 crossed array, with each trap separated by one metre. Each nine-trap array was considered as one sampling unit and was positioned within the quadrat using randomly created coordinates. Pitfall traps were polyethylene plastic vials, 50 mm in diameter and 150 mm in depth, placed within orange electrical conduit PVC sleeves and filled with 50 ml of a 70:30 ethanol/water solution. They were set flush with the ground and a square rain cover was suspended about 5 cm above each. Pitfall traps were left open for nine days and catches from all nine traps at each plot were pooled before analyses. The trapping methods are described in detail in Kitching *et al*. (2005).

We conducted pitfall trapping in October 2006 and February 2007, and catches from these two sampling occasions were combined before analyses. All spiders (Araneae), ants (Formicidae, only workers) and beetles (Coleoptera) were extracted from traps and sorted to species or morphospecies by CJB (ants), RJR (spiders) and KMS (beetles). In this study we considered all spider and ant species to be predatory and only beetles from families known to consist primarily of predatory taxa according to Lawrence & Britton (1991) were included in analyses. Voucher specimens were deposited in the Queensland Museum, Brisbane (ants and spiders) and the Arthropod Biodiversity Laboratory, Griffith University, Nathan, Queensland (beetles).

Data analysis

To investigate sampling sufficiency of the three arthropod groups, we first generated individual-based species accumulation curves using the expected richness function (Coleman curves) available from EstimateS software ver. 8.2 (Colwell 2009). Individual-based rarefaction curves represent expected species density, given n individuals. Species richness of local arthropod communities was also estimated using the Abundance-based Coverage Estimator (ACE) which estimates the number of species by taking unseen species (i.e. species not collected) into consideration.

To test for differences in species richness and total abundance of the three arthropod groups among different elevational zones, single-factor ANOVAs were performed with SPSS ver. 13.0 (SPSS Inc. 2004). For *post-hoc* pairwise comparisons we employed Tukey HSD tests. All abundance data were log-transformed before analyses.

To examine changes in the composition of arthropod assemblages across altitude, we used principal coordinates analysis (PCO) available in PERMANOVA+ (Anderson *et al*. 2008) to generate an ordination for each arthropod group. Instead of conventionally used

TABLE 1. Number of species and individuals of each genus (ants) and family (predatory beetles and spiders) of the three predatory arthropod groups sampled.

Ant genus	No. species	No. individuals
Amblyopone	1	1
Anonychomyrma	2	44
Camponotus	1	1
Carebara	2	28
Cerapachys	1	1
Colobostruma	1	1
Crematogaster	2	17
Discothyrea	1	1
Heteroponera	1	2
Hypoponera	2	9
Leptogenys	4	54
Leptomyrmex	2	6
Lordomyrma	1	1
Mayriella	3	11
Monomorium	7	42
Myrmecina	1	4
Notoncus	1	22
Notostigma	1	3
Pachycondyla	2	4
Paraparatrechina	1	1
Pheidole	7	685
Ponera	1	1
Prionopelta	1	5
Pristomyrmex	1	3
Prolasius	5	80
Pseudonotoncus	1	1
Rhopalothrix	1	1
Rhytidoponera	2	280
Solenopsis	1	250
Sphinctomyrmex	1	1
Strumigenys	2	2
Tapinoma	1	1
Technomyrmex	2	3
Total	**63**	**1566**

Beetle family	No. species	No. individuals
Carabidae	16	58
Coccinellidae	1	1
Scydmaenidae	11	28
Staphylinidae	82	1635
Total	**110**	**1722**

Spider family	No. species	No. individuals
Amaurobiidae	6	88
Amphinectidae	1	9
Anapidae	2	97
Barychelidae	1	13
Clubionidae	3	10
Cycloctenidae	7	156
Desidae	2	14
Dipluridae	1	2
Gnaphosidae	3	28
Gradungulidae	1	9
Hahniidae	1	1
Hexathelidae	1	1
Idiopidae	1	3
Lamponidae	3	10
Linyphiidae	9	61
Liocranidae	1	1
Lycosidae	7	90
Malkaridae	1	14
Micropholcommatidae	2	3
Mimetidae	1	1
Mysmenidae	1	66
Nemesiidae	5	27
Nicodamidae	1	2
Oonopidae	6	62
Orsolobidae	1	12
Pisauridae	1	2
Salticidae	10	33
Sparassidae	4	22

TABLE 1. cont...

Spider family	No. species	No. individuals
Stiphidiidae	2	3
Tengellidae	2	7
Textricellidae	1	1
Theridiidae	6	28
Theridiosomatidae	1	2
Thomisidae	1	11
Trochanteriidae	2	3
Zodariidae	3	27
Zoridae	2	49
Zoropsidae	2	4
Total	105	972

TABLE 2. *F* and *P* values of the effect of elevational differences on the total abundance, species richness and assemblage composition of the three predatory arthropod groups. Parametric ANOVA was conducted on total abundance and species richness, whereas permutational multivariate ANOVA (PERMANOVA) was conducted on assemblage composition. Significant *P* values are shown in bold.

	F (pseudo-F)	P
Total abundance		
Ants	22.12	**<0.001**
Predatory beetles	2.07	0.137
Spiders	1.75	0.192
Species richness		
Ants	21.61	**<0.001**
Predatory beetles	5.24	0.008
Spiders	3.12	0.047
Assemblage composition		
Ants	4.63	**<0.001**
Predatory beetles	3.37	**<0.001**
Spiders	3.21	**<0.001**

non-metric multidimensional scaling (NMDS) ordination, we used PCO because the scales of the resulting PCO axes are interpretable in the units of the resemblance measure (Anderson *et al*. 2008). Primary and secondary axes

(which generally explain a large proportion of the variation in assemblage composition) were used to generate two-dimensional ordinations. Primary axis values were also plotted against the actual altitudes of the sampled plots to compare how assemblage composition changed with increasing altitude among the three arthropod groups. Abundance data were square-root transformed prior to analyses and the Bray-Curtis index was used to quantify similarities in assemblage composition between samples. Due to the extremely low abundance of ants at one of the 1100 m plots (1% of the total ant abundance) it was removed from the multivariate analyses of ant assemblages. We tested the influence of altitude on assemblage composition using PERMANOVA (permutational multivariate analysis of variance) available in PERMANOVA+ (Anderson *et al*. 2008). PERMANOVA calculates *F* statistics (pseudo-*F*) based on a chosen distance measure of assemblage composition (Bray-Curtis index here), and obtains *P* values using permutation techniques (4999 unrestricted permutations of raw data). Altitude was incorporated in the analyses as a fixed factor and Type III Sums of Squares was used to calculate pseudo-*F* statistics.

RESULTS

Overall composition

The predatory guild comprised of ants, predatory beetles and spiders was represented by a total of 4260 individuals (Table 1). Ants, 1566 specimens of 63 species, accounted for 37% of the total individuals. Ants were dominated by the genus *Pheidole*, which consisted of seven morphospecies and accounted for 44% of the total ant abundance. Predatory beetles consisted of 1722 individuals (40% of all predators) and 110 species. Staphylininae comprised the largest proportion of the predatory beetles (Table 1). Spiders were represented by 972 individuals (23% of all predators) from 105 species. The single species of Cycloctenidae (*Cycloburra* ibi9) was the

most abundant species contributing 13% to the total spider abundance.

Individual-based species accumulation curves for ants and spiders showed gradual abatement in the incline of the slopes towards the end of the curves (Fig. 1). This, however, was not the case for predatory beetles with the species accumulation curve still sharply increasing. Accordingly, there were smaller differences between estimated (ACE) and observed species richness for ants (estimated = 91 species versus observed = 63) and spiders (138 vs 105), whereas more than twice as many species were estimated than observed for predatory beetles (258 vs 110).

Elevational patterns

Total abundances of all three arthropod groups did not vary greatly between elevational zones, with the exception of 1100 m a.s.l., where ant abundance declined sharply and significantly (Fig. 2; Table 2). Unlike total abundances, species richness of all three arthropod groups was significantly influenced by altitude (Table 2). Post-hoc tests showed a gradual decline in ant species richness with increasing altitude (Fig. 2). Beetle species richness significantly peaked at mid-elevations with greater species richness at 700 and 900 m a.s.l. Due to a marginally significant ($P = 0.047$) effect of altitude on spider species richness, none of the pair-wise comparisons were significantly different (Fig. 2).

All three arthropod groups progressively changed assemblage compositions from 300 to 1100 m a.s.l. (Fig. 3). The results of PERMANOVA concurred with these observed patterns, showing a highly significant effect of altitude on the assemblage composition of all three predatory groups. The fine scale patterns of their responses to altitude were, however, different (Fig. 4). Ants displayed an almost linear relationship between the primary PCO axis values and altitude. Primary PCO values of beetles gradually declined from 300 to 900 m a.s.l. and then sharply dropped at 1100 m a.s.l. In contrast, spiders did not exhibit clear elevational

patterns at lower elevations but there was a prominent discrepancy in primary PCO values between lower (300-700 m a.s.l.) and higher (900, 1100 m a.s.l.) altitudes.

DISCUSSION

The steep slope at the end of predatory beetle species accumulation curve, reinforced by the estimated beetle species richness at more than double the observed richness, suggests that this arthropod group was substantially under-sampled in our study. This is attributable to the fact that most beetle species were represented by singletons and doubletons (76 of a total of 110 species, 69%) with few common species (13 species represented by more than 10 individuals). Ants and spiders appeared to be more adequately sampled, although estimated species-richness was 44% and 29% higher than observed richness respectively. Despite potential under-sampling, assemblage composition of all three predator taxa responded clearly to changes in altitude. Although increased sampling intensity may have yielded more species, we believe that the overall patterns of predatory taxa would not differ substantially from those we observed in this study.

Of the three arthropod groups sampled, ants responded most strongly to altitude. Although the abundance of ants was more or less similar across most of the gradient, there was a sharp and significant reduction in ant abundance at the highest elevation. Ant species richness and assemblage composition changed across the entire gradient, with a decline in richness (Fig. 2) and progressive change in ant assemblages (Figs 3, 4) from low to mid to high altitudes. These results mirror those of other studies on ants along the IBISCA-Queensland transect (Burwell & Nakamura 2009, 2011). Burwell and Nakamura, who sampled ants more intensively, targeting ground, litter and arboreal habitats, also found markedly less ants at 1100 m a.s.l., and a gradual decline of species richness and progressive changes in assemblage composition
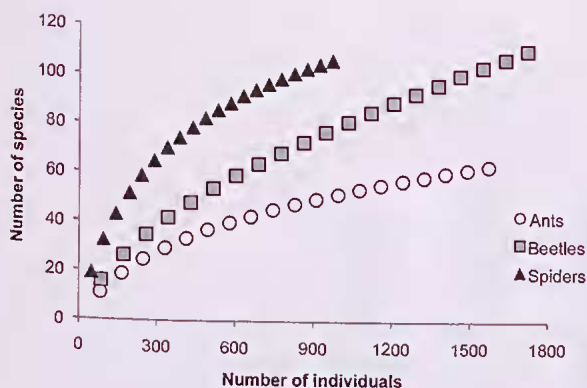
FIG. 1. Individual-based species accumulation curves of ants, predatory beetles and spiders collected in pitfall traps from the IBISCA-Queensland transect in Lamington National Park.

with increasing altitude. In addition, Bito *et al.* (2011) found significant decline in ant predation pressure at ground-level, measured as the proportion of tuna baits occupied by ants, along the IBISCA-Queensland transect. Similar declines in ant species richness and abundance with increasing altitude have been documented elsewhere (Olson 1994; Bruhl *et al.* 1999). Hodkinson (2005) suggested that ants, in general, are characterised by depauperate assemblages at higher elevations.

Ants are known to be sensitive to changes in climatic conditions (Sanders *et al.* 2007). Indeed, the observed responses of ants in our study were consistent with changes in climatic conditions measured along the IBISCA-Queensland gradient. Gradual changes in ant species richness and assemblage composition paralleled gradual decline of median temperature with increasing altitude (Strong *et al.* 2011). In addition, rainfall is higher at higher elevations in the region (Strong *et al.* 2011) and areas above around 900 m a.s.l. receive additional moisture inputs via cloud-stripping (Laidlaw *et al.* 2011b). Consequently soil moisture increases with increasing elevation, and at 1100 m a.s.l. high soil moisture is maintained throughout the year

(Strong *et al.* 2011). Low temperatures at high elevations combined with reduced insolation associated with increased cloud cover (Rahbek 1995) have been suggested to reduce foraging time for ants and slow their developmental rates (Fisher 1998). High soil and litter moisture levels at high elevations have also been suggested to reduce the availability of nest sites, and to interfere with the foraging activity of small ants (Bruhl *et al.* 1999). Thus the colder and, particularly, the wetter conditions at the highest altitude most probably account for its depauperate ant fauna.

Predatory beetles showed a mid-altitudinal peak in species richness, and both species richness and abundance at the highest elevation (1100 m a.s.l.) were comparable to those found at lower elevations. Assemblage composition of predatory beetles progressively changed from low to mid-elevations, but those found at 1100 m were dramatically different from lower elevations. Unlike ants that had very depauperate assemblages at the highest elevation, beetles at this elevation were characterised by many species unique to this particular elevation (12 species). Although our results need to be interpreted carefully due to possible undersampling, the observed patterns were consistent with those found by Ødegaard and Diserud (2011) who conducted more extensive surveys of beetles in the understorey vegetation within the same survey plots.

In contrast to ants and beetles, both the species richness and abundance of spiders were only weakly related to altitude. Altitudinal changes in spider assemblages were idiosyncratic with a clear separation between assemblages from lower (viz. 300, 500, 700 m a.s.l.) and higher (viz. 900, 1100 m) elevations. Unlike beetles, there were few high altitude specialists among the spiders; only four species were restricted to 1100 m a.s.l. An altitudinal study in rainforest in tropical Queensland found lower level of species turnover among spiders compared with beetles (Monteith & Davies 1991). Similarly, spiders exhibited
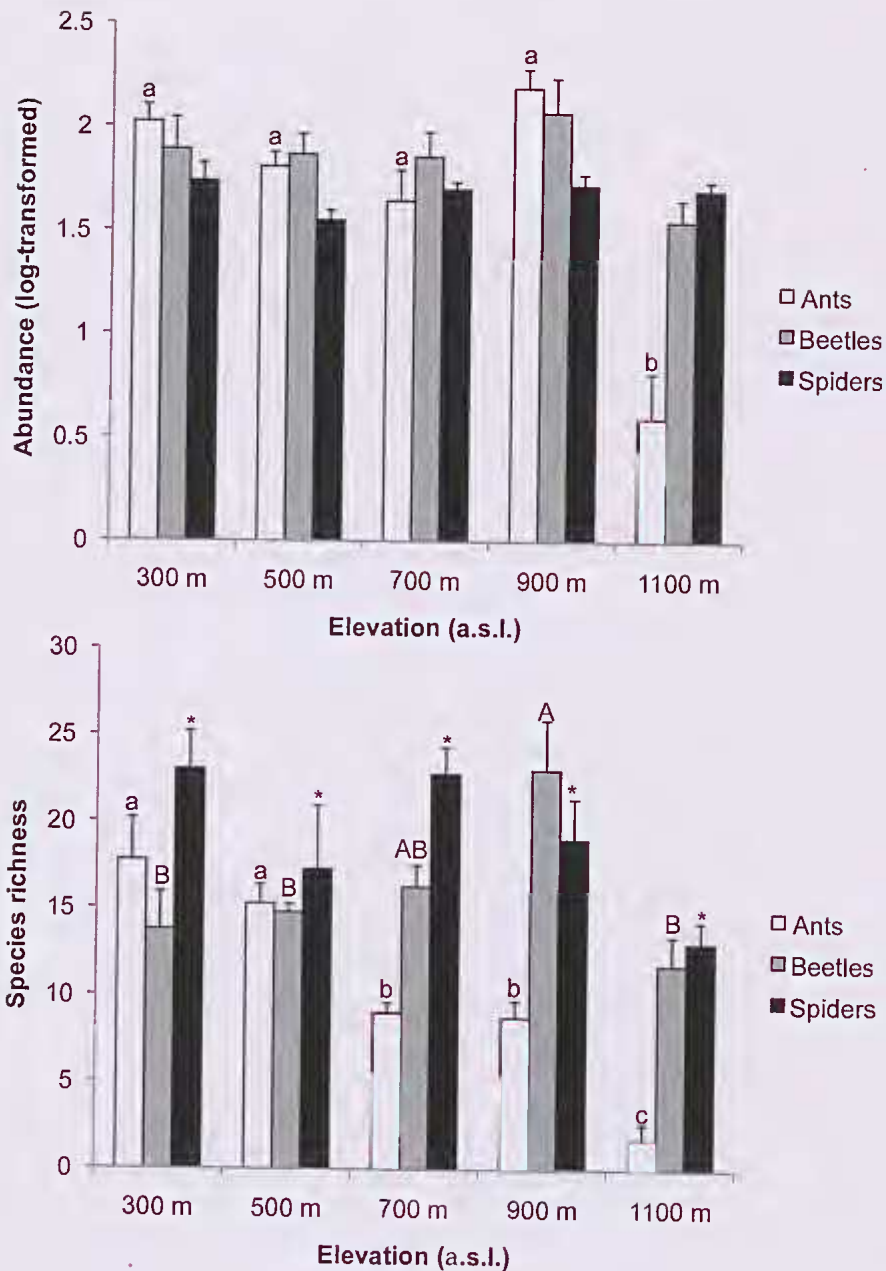
FIG. 2. Mean (+SE) total abundance (log-transformed) and species richness of ants, predatory beetles and spiders collected in pitfall traps across five elevational zones in Lamington National Park. Results of post-hoc pair-wise comparisons are shown using different letters to indicate significant differences between elevational zones. Lower case letters are for ants and upper case letters for predatory beetles. * Although the main factor was significant for spiders, none of the pair-wise comparisons displayed significant differences due to only a marginal effect of the main factor (*P*=0.047).
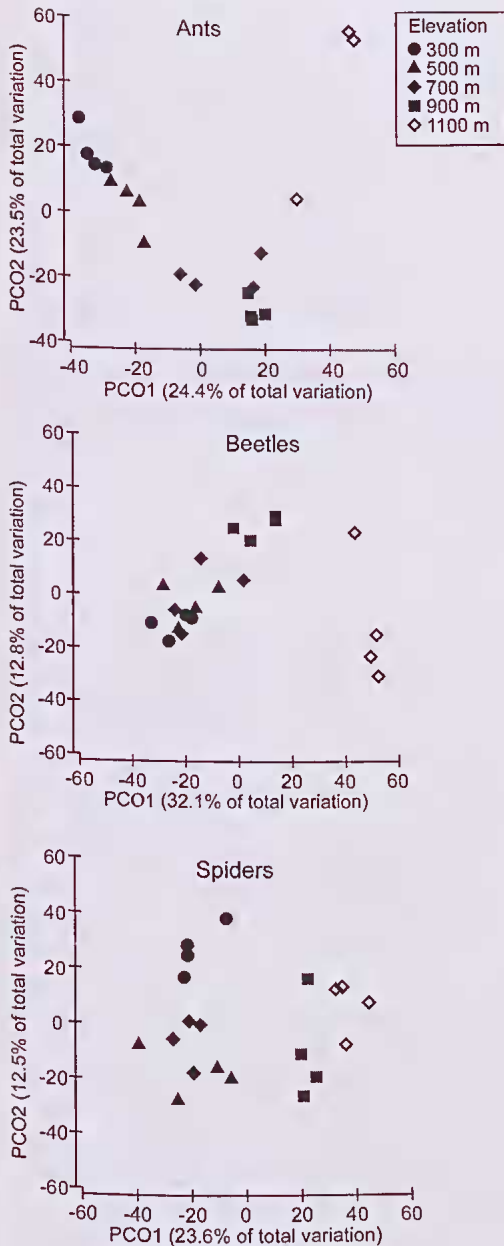
FIG. 3. PCO ordinations based on ant, predatory beetle and spider species assemblages (square-root transformed) across the five elevational zones, showing the primary and secondary axes values. Total variation of the assemblage composition explained by each axis is also displayed.

comparatively low species turnover among different forest types (Oliver & Beattie 1996b). Perhaps spiders are more tolerant to changes in habitat conditions, and in general spider species may display broader altitudinal ranges compared to ants and beetles.

Despite significant responses to altitude in the assemblage composition of all three taxa examined here, their response patterns were distinctive (Fig 3), suggesting limited surrogacy among these predatory arthropod groups. Studies attempting to assess the impacts of future climate change on ecological processes such as predation, must be mindful that predictions based on one taxonomic group may not apply to other groups. For example, consider potential changes in the predator landscape at the highest elevations of the IBISCA-Qld transect (1100 m a.s.l.) under moderate warming of about 1.5°C. With an increase in temperature of that magnitude, organisms would be predicted to shift their distributions upslope by around 200 m. If we first consider spiders, we would predict little change as spider abundance, richness and assemblage composition is currently similar at 900 and 1100 m a.s.l. For beetles, predation pressure may change little as overall abundances are currently similar at 900 and 1100 m a.s.l. However, the composition of predatory beetles may shift substantially, with the potential loss of many high altitude restricted species, but an overall increase in species richness as a greater number of species from 900 m a.s.l. move upslope. With regards to ants, a future scenario may be dramatically different, where the now depauperate ant fauna at 1100 m a.s.l. is replaced by a suite of additional species found at 900 m a.s.l., and most importantly overall ant abundance, and hence predation pressure, would be expected to increase dramatically.

These 'just-so' predictions are, however, oversimplifications and inter- and intra-guild interactions will complicate climate change impacts. Predatory beetles have been suggested to be susceptible to competition from ants (Darlington 1943; Reznikova & Dorosheva

2004, Hawes *et al.* 2002). In high elevation rainforests abundant carabid populations have been attributed to a coincidental scarcity of ants (Darlington 1971; Olson 1994). Potential invasion of the highest elevations (primarily by ants) at Lamington National Park may consequently impact upon resident predators, particularly carabid beetles.

The observation that different predatory groups respond in contrasting fashions to climatic changes (as reflected by adjacent altitudes) underlines the need for the use of multiple taxa in biodiversity monitoring programmes. Such prescriptions may test the availability of financial and expert resources yet are clearly essential.
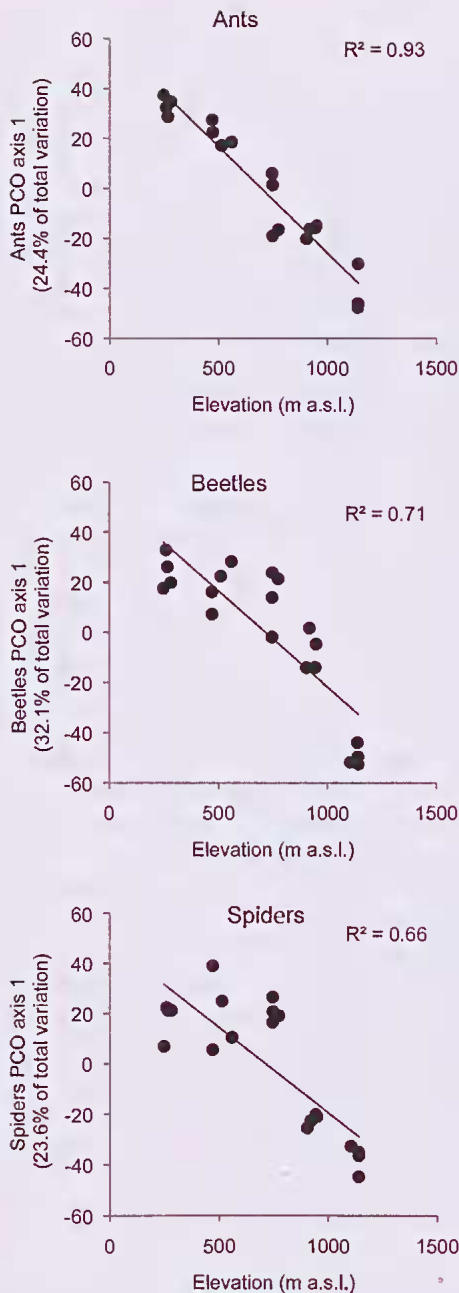
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FIG. 4. Values of the primary PCO axis plotted against actual altitudes of the survey plots for ants, predatory beetles and spiders. A straight line was also fitted with the R^2 value for each arthropod group.

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